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Links from Mantle to Microbe at the Lau Integrated Study Site: Insights from a Back-Arc Spreading Center

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ADD ABSTRACT

INTRODUCTION

A central aim of the Ridge 2000 Program is to understand the flow of energy and mass from Earth's deep mantle to the seafloor and ocean, and how this flow influences deep-sea biological communities. Among the three designated sites for intense studies, the Lau Integrated Study Site (ISS) provides unique opportunities that derive from the back-arc tectonic setting of this spreading center. Back-arc spreading ridges are influenced by the flux of water and other elements derived from the down-going lithospheric slab (brittle portion of the descending crust and mantle; Figure 0). These elements are most prominently displayed in the lavas of the volcanic front that occur ~110 km above the slab. In regions of extension, back-arc basin spreading centers open behind the volcanic front. Because back-arc ridges are often oblique to the arc, they sample the mantle at varying distances above the slab and receive an "arc geochemical signal" that decreases with distance from the volcanic front of the arc. This arc signal prominently includes water, which has a major effect on mantle melting and differentiation, and also other volatiles and elements such as CO₂ and S that play major roles in biological processes.

The tectonic and geographic setting of the Eastern Lau Spreading Center (ELSC) and Valu Fa Ridge (VFR) provide some valuable opportunities for the study of ridge processes. In particular, the contrast in lava compositions relative to MORs, and the gradients in ridge characteristics, which result from the oblique configuration of arc and spreading center, provide a natural experiment on how differences in ridge characteristics influence life. In addition, the location of the ridge in the western Pacific allows study of a biogeographical province that is different and distinct from those of eastern Pacific and mid-Atlantic ridges.

These opportunities have lead to a rather different approach than has been taken at the East Pacific Rise (EPR) at 9°50'N and the Endeavour Segment of the Juan de Fuca Ridge ISSs

(see Fornari et al., 2012, and Kelley et al., 2012, both this issue). At the Lau ISS, a regional perspective was taken to permit study of the range of vent fluid, chimney and lava compositions, and associated biological communities, and how they respond to changing ridge characteristics. To exploit these opportunities also provided an exceptional logistical challenge. In comparison to the Endeavour and EPR 9°N ISSs, there was a relative lack of information about the ELSC, since it did not have the decades of previous intensive work that characterized the other two ISSs. The challenge, which was successfully met by using a carefully coordinated series of staged voyages, was to explore and investigate a significant length of ridge, find hydrothermal sites and carry out meaningful integrated studies on the limited time-frame of the R2K program.

Initial work consisted of four cruises in 2004 and 2005. The first mapped the ELSC and VFR, obtained water column profiles to locate the regions with most intense hydrothermal activity (Baker et al., 2006; Martinez et al., 2006; Figure 1), and deployed floats to study the deep flow field in the Lau Basin (see Speer and Thurnherr, 2012, this issue). The second obtained rock samples along the length of the ridge, and used the ABE autonomous benthic explorer and the TowCam digital deep-sea imaging system (Fornari, 2003) to discover three new hydrothermal sites along the ELSC (Kilo Moana, TowCam, ABE) (Bezos et al, 2009; Escrig et al., 2009; German et al., 2008), and collaborate in the discovery of the Mariner vent field on the VFR with Japanese scientists who were in the area at that time. The third used the ROV Jason to map the vent fields, photograph biological communities and sample hydrothermal fluids and deposits, as well as discover an additional vent site (Tui Malila) (Ferrini et al., 2008). The fourth cruise then carried out more detailed biological and coupled biological and chemical studies of the vent sites. Follow-on studies included a large seismic experiment to more thoroughly investigate mantle processes using passive and active seismic techniques that was undertaken

during 2009 and 2010, and additional detailed microbial, biological and biogeochemical field work conducted in 2009 using Jason. The latter provided a temporal component to biological and vent geochemical studies. In addition, further plume mapping of a section of the ELSC (from 19.9deg S to 21degS) and of the VFR (21.9 to 22.4S) was carried out in 2008 (Baker et al., 2010). Results of those surveys include successful mapping of plumes, all occurring within ~1.5 km of the ridge axis, with no detection of plumes farther off-axis, and detection of oxidation-reduction potential anomalies on the VFR consistent with the presence of low-temperature hydrothermal sources on the axial flank.

CHARACTERISTICS OF THE ELSC/VFR

Ridge Morphology and Petrology

The Lau ISS is located between 19°20'S and 22°45'S along the ELSC and VFR (Figure 1). Along this distance of ~240 km, the spreading center and ridge exhibit systematic changes in a number of variables from north to south. The lateral and depth distances to arc magma sources vary substantially (i.e., slab; Figure 0), the spreading rate decreases from 95 mm/yr to 40 mm/yr (full rate), and axial depth decreases from 2700 m to 1740 m. From north to south the spreading ridge morphology changes from a highly faulted axial valley to an inflated axial ridge, and the seismically detected “lens” of melt in the crust beneath the spreading axis varies from being absent or only present as isolated melt sills to continuously present. Crustal thickness along axis increases from about 5 to 7.5 km, and lava chemistry changes from compositions that include tholeiitic basalts that are depleted in elements like Ba, Rb, La, Th, and U (similar to mid-ocean ridge basalts) to more andesitic compositions with a strong arc geochemical signature (i.e., enriched in the above elements) (Pearce et al. 2004; Peate et al. 2001; Martinez et al., 2006; Jacobs et al., 2007; Bezos et al., 2009; Escrig et al., 2009).

These characteristics have some surprising contrasts with mid-ocean ridges (MORs). For most MORs, as spreading rate declines the ridge morphology changes from an axial high to an axial rift and the intensity of faulting increases. In contrast, the slower spreading, southern portions of the ELSC/VFR are characterized by shallow axial highs and minimal faulting, while the fastest spreading portions exhibit deeper rift valleys with flatter axes and a greater faulting intensity (Martinez et al., 2006) (Figure 1). There is a rather abrupt transition between the two types of ridge morphology near 20°35'S, over a distance of about 20 km along a short segment in the middle of the study region.

While there is insufficient sampling to fully explore the time dimension, in general terms of change in subduction component the north-south morphological changes that are observed along the ELSC/VFR are also observed across the axis (which is the time dimension). Back arc spreading centers are much less stable than MORs. Ridges are born and propagate and die over periods of a few million years, changing the spatial relationship of the ridge to the arc and slab. In the Lau Basin the ridge has steadily propagated southwards. As it propagated, the location of the ridge with respect to the arc became increasing distal with increasing distance behind the propagating tip. Thus, with age, seafloor spreading separates the ridge from the Tofua arc, isolating it from the water flux from the slab that enhances mantle melting and leads to more voluminous and compositionally distinct magmas (Figure 0). New geophysical data show that one million years ago, the northern part of the ELSC looked physically more like the ridge to the south, with more rugged bathymetry and thicker, lower density (probably andesitic) crust (Dunn and Martinez, 2011). Preliminary geochemical data for rocks collected off-axis show this is likely (P. Michael, unpub. data). The change is rapid, as it is along the axis, suggesting to Dunn and Martinez that there is a threshold effect related to the distance to the arc.

As noted, observed morphological differences in the Lau basin correlate with compositional differences. Along the ELSC/VFR axis, changes in ridge morphology correspond with large changes in the temperatures, compositions and amounts of crystallization experienced by the erupted lavas (Figure 2). As magmas ascend into cold crust, their temperature decreases and they crystallize, causing their MgO contents to decrease. For normal MORs, MgO decreases with very little increase in SiO₂. At convergent margins, however, decreasing MgO is associated with a marked increase in SiO₂, leading to the succession of lava types: basalt-andesite-dacite-rhyolite. This difference is reflected in the change in differentiation path along the ELSC and VFR. In the north, high temperature basaltic lavas with ~8 wt.% MgO make up most of the recovered samples, and SiO₂ does not change much as MgO decreases. Over the restricted region where there is an abrupt change in axial morphology (near 20°35'S), the lavas become andesitic as the MgO content drops (Figure 2a). Lavas in this region generally have less than 5.5% MgO, and higher SiO₂. Further south, along the VFR, dacites (lavas with >59% SiO₂ and with only 2-3 wt.% MgO) are a significant component of the recovered rocks. Thus the path of differentiation changes from one similar to ocean ridges far from the subduction setting, to one more similar to arc lavas.

Along with these changes in rock type and inferred eruptive temperature, there are large changes in the concentrations of trace elements that reflect the flux of material (e.g., H₂O, Ba, Th, and to a lesser extent, La) from the down-going slab (Figure 0), with concentrations increasing markedly southwards. The various elements are tracers of the materials of the down-going slab and the processes that transport them. For example, Th is an element with high concentrations in sediment that is insoluble in hydrous fluids, while Ba is both high in sediments and easily transported by fluids. Changes in the various ratios of these tracers thus give an

indication of materials and processes at depth. Generically these tracers are called “subduction components.”

If there were simply a homogeneous subduction component increasing in strength as the ridge approaches the arc, then we would expect smooth increases in ratios and concentrations moving southwards along the ridge. While there is an overall increase from north to south, the changes are not a smooth gradient and show that there is not a single subduction component (see Figure 2). There are two geochemical transitions: one at $\sim 20.6^{\circ}\text{S}$ characterized by a jump in Ba/Th, Th/La, and La/Sm, and another between $\sim 21.07^{\circ}\text{S}$ and 21.21°S that is more gradual with a decrease in Ba/Th and increases in Th/La, La/Sm, and $^{206}\text{Pb}/^{204}\text{Pb}$, but not Ba/Nb (Escrig et al., 2009). There is clearly some process at depth that leads to a preferential enrichment of Ba relative to Th mid-way along the ridge (Figure 2b). The more northern transition correlates with the change in ridge morphology from an axial rift valley to an axial high, and the decrease in MgO and increase in SiO_2 that marks the change from basaltic to andesitic crust noted above (Escrig et al., 2009).

One of the notable results of the closely spaced rock sampling carried out in 2005 is the correspondence between geochemical signals along the back-arc spreading center and the position of volcanoes along the volcanic arc. Pb isotope ratios undulate along the back-arc in conformity with the positions of arc front volcanoes, and the complex mixing trajectories leading to the irregular along-axis patterns of trace element ratios result from mixing towards distinct compositions of volcanoes from the arc (Escrig et al, 2009). The change in chemical compositions then relates in part to the distance of the back-arc spreading center from the arc, and in part to whether the back-arc is directly behind an arc volcano or not. This result is particularly intriguing in light of seismic evidence that suggests substantial horizontal mantle

flow parallel to the volcanic front (Smith et al 2001; Conder and Wiens, 2007). A possible solution is that the flow of slab-derived hydrous fluid and wedge-derived melt is rapid relative to solid mantle flow so that the mantle flow does not offset the position of the fluid flux.

The hydrous fluid flux from the slab to the mantle is critical to the overall behavior of the back-arc spreading center. Water lowers the mantle's melting temperature, increasing the extent of partial melting and melt production, and therefore increasing crustal thickness. Water contents of basalts are lowest on the northern ELSC and increase toward the VFR in the south, as the distance to the arc decreases. Crustal thickness increases from ~5.5 km beneath Kilo Moana vent field in the north to 7-8 km beneath Mariner vent field in the south (Collier and Sinha, 1992; Jacobs et al., 2007). The higher water content also causes basaltic magmas to evolve to more silica-rich andesites and dacites as they cool. This may be particularly important at Mariner vent field, which has dacitic lavas and basalts in close proximity. These changes in magma supply and composition conceptually could lead to the changes in the depth and shape of the ELSC/VFR noted above that are opposite what is observed at normal MORs (Martinez et al., 2006; Figure 1). The deeper, rifted, fast-spreading northern part of the ELSC would have the normal characteristics of an intermediate MOR owing to low water content. The slower-spreading VFR in the south would have the characteristics normally associated with a fast-spreading MOR because of the increased flux caused by increased water content.

Since the water also affects the path of differentiation and the viscosity and temperature of erupted lavas, these changes also influence the physical characteristics of the crust, which in turn can impact hydrothermal systems. Seismic velocities of the crust in the north are similar to those of MORs (5-6 km/s at 1 km depth), but those on the VFR in the south are slower (~4 km/s at 1 km depth; REF). The slow velocities could be due to greater porosity of the crust, owing to

higher vesicle content from the higher water contents of the lavas (Carlson and Herrick, 1990). Another factor could be the higher SiO₂. Either way, the slow velocities are outside the behavior of normal MORs, and a direct response to a changing volatile content associated with the arc influence.

These hypotheses of possible relationships between hydrous fluid flux from the slab to the mantle and ridge morphology can be tested further by qualitative and quantitative models. Dunn and Martinez (2011) propose a qualitative model with a narrow ridge melting regime where the melting regime becomes abruptly disconnected from the arc flux, leading to the rapid change in the physical and chemical characteristics of the ELSC near 20.6°S. This model, however, has difficulty accounting for the clear existence of a continuing arc signature to the north of this boundary. Harmon and Blackman (2010) have constructed quantitative 2-D models for the various spreading centers of the back-arc basin. Their models produce a wide melting regime and do not reproduce the abrupt change close to the arc proposed by Dunn and Martinez (2011). They are able to produce a substantial change in crustal thickness between the VFR and the ELSC, but the overall thicknesses exceed the observations. Since the variations in arc flux are clearly three dimensional (Escrig et al. 2009), results from 3-D modeling studies will be an important step forward.

In terms of mantle impact on hydrothermal and biological systems, an important difference between the northern and southern parts of the ELSC/VFR is the contribution from the magmas to hydrothermal fluids, both through release of volatile species during magmatic degassing, and through reaction between seawater and the solidified igneous rock (Mottl et al., 2011). As magmas ascend, they decompress and become oversaturated with vapor. They produce additional vapor as they crystallize in the axial magma chamber. Beneath the northern vent fields

(TowCam, Kilo Moana) MOR basalt (MORB)-like magmas release mostly CO₂ into hydrothermal systems (REF). Beneath the southern hydrothermal vent fields, H₂O-rich magmas release mostly H₂O to hydrothermal systems. Moreover, as H₂O exsolves from the magma, it carries CO₂, but also sulfur gases (REF). These gases (e.g., SO₂) can affect the composition of hydrothermal fluids and are available for biological activity at the seafloor. The magmatic gases present in some back-arc environments, particularly SO₂, can influence the pH and other chemical parameters of the fluids and result in differences in vent deposit composition, as discussed in more detail below.

Accompanying water from the subducting slab into the mantle wedge and thence to the magmas and crust are other elements that are far in excess of their concentrations in MORB, notably Ba and Pb. Reaction of evolving hydrothermal fluids with these enriched igneous rocks results in vent fluids enriched in some elements (e.g., Ba, Pb, As) relative to vent fluids present at MORs, and the compositions of hydrothermal mineral deposits at the Lau vent fields reflect these chemical differences (Tivey et al., 2005; Lau Workshop Report, 2006). Barium in particular plays an important role, with the mineral barite (BaSO₄) being stable under seafloor conditions, and resulting in vent deposits with greater structural integrity than many found at vent fields along MORs.

The ratio of volatiles (e.g., H₂O, CO₂, SO₂, H₂S) to other elements may be a critical aspect of the influence of magma compositions on the hydrothermal systems, both through addition of volatiles, and from seawater/rock reaction. While it is possible to measure primary water contents for the lavas from the northern part of the study area, the lavas from the south are sufficiently water-rich and the ridge sufficiently shallow that primary water compositions cannot be obtained from the lavas themselves. In the north, however, Bezos et al. (2009) were able to

obtain the compositions of the hydrous fluids that were contributing to the (low amplitude) arc signature that is nonetheless present there. One of the striking results is that the ratio of H₂O to trace elements in basaltic glasses along the ELSC is much higher than it is for a similar calculation carried out for the Marianas arc (Stolper and Newman, 1994). This result can be understood from the effect of temperature on characteristics of fluids coming off the slab (Kessel et al., 2005). At low temperatures, trace elements have low solubility in hydrous fluids. As the temperature increases, the solubility increases by orders of magnitude. One of the features of the ELSC is the very fast convergence rate of the down-going Pacific plate. This fast convergence carries a low temperature slab to greater depth faster, leading to a slab environment beneath the arc and back-arc that is cool relative to other arcs. Other back-arcs have slower convergence, and slab temperatures may be higher, leading to a different relative flux of volatiles to other elements. These results suggest that different back-arc basins may have distinct system-wide responses to the arc influence.

Newly Discovered Vent Fields

A major goal of Lau ISS studies was discovery of additional vent fields, particularly along the ELSC. Vent fields had been identified prior to 2000 along the VFR (e.g., Fouquet et al, 1991), but not along the ELSC. Nine previously undiscovered vent fields have been located along the ELSC/VFR since 2004, six as part of R2K studies, three as part of commercial ventures, making it possible to investigate links between crustal and hydrothermal vent fluid compositions. Areas along the spreading-axis where venting was occurring were each located beginning initially using towed CTD (conductivity, temperature depth) plume data (Baker et al., 2006, 2010). Discovery of the ABE, Kilo Moana and TowCam sites (Figure 1) was facilitated by use of a nested discovery process using the ABE vehicle and a towed digital deep-sea camera

(German et al., 2008). The Tahi Moana 1, Tui Malila, and Mariner vent fields were found by more traditional techniques such as tow-yos, camera tows, and follow-up remotely operated vehicle or human occupied submersible dives (Ishibashi et al., 2006; German et al., 2008; Ferrini et al., 2008; SRK Consulting report for Nautilus Minerals, 2008; Figure 1). Three additional sites, TELVE, Si'I Si'I, and Misiteli, were discovered using plume data from Baker et al. (2006, 2010) as part of surveys conducted by Nautilus Minerals, for commercial interests and have not been subject to R2K studies (SRK Consulting report for Nautilus Minerals, 2008).

Ultrahigh-resolution (sub-meter) near-bottom multibeam bathymetric mapping of six of the known vent fields (Kilo Moana, TowCam, ABE, Tui Malila, Mariner, Vai Lili) have documented dimensions and spatial relationships among tectonic, volcanic and hydrothermal features. The two northernmost vent fields, Kilo Moana and TowCam, are located at similar depths (~2620 m and ~2700 m, respectively), and hydrothermal activity is and has in the past been associated with faults and fissures that crosscut broad, low relief volcanic domes and pillow and lobate flows (Ferrini et al., 2008). The igneous host for these fields are the high MgO, incompatible element depleted samples documented above (Escrig et al. 2009; Bezos et al 2009). The Tahi Moana 1 vent field is located at a depth of ~2230m, ~41 km south of the TowCam vent field, and ~9 km north of the ABE vent field on a separate ridge segment (Figure 1), but detailed mapping has not yet been done. Of interest is that this vent field is located very close (20.66°S) to the petrologic transition observed at ~20.6°S (Escrig et al., 2009; Figure 2).

The ABE and Tui Malila vent fields are hosted in terrain that exhibits more variable and complex volcanic morphology than within the Kilo Moana and TowCam vent fields, and differs considerably from that at MORs. There are high aspect ratio volcanic domes within and proximal to the vent fields along with pillow flows, aa-type lavas, and distinct finger-like flows, likely

reflecting the effects of higher lava viscosity on transport and deposition of flows (Ferrini et al., 2008). While these vent fields are located at significantly different depths (~2140 m versus ~1720 m, respectively) on two different spreading center segments, both are hosted in substrate ranging from basaltic andesite to andesite. At the Mariner vent field (and the Vai Lili vent field 4 km to the south), located on the VFR very near the overlapping spreading center at 22°10'S, the volcanic morphology is dominated by small (tens of meters diameter) domes and lava flows, but an absence of crosscutting faults or fissures (except for a single identified fault within the Vai Lili vent field); volcanic relief is greater than that within vent fields to the north, and aa-type lava flows dominate, consistent with more viscous lavas (Ferrini et al., 2008). Silica contents of lavas recovered in 1989 from near the latitude of these vent fields indicate rocks of basaltic-andesite and andesite composition, with some basalts and dacites also recovered (Fouquet et al., 1993).

Sampling and analysis of vent fluids from each of these vent fields has identified some correlations between igneous rock composition and vent fluid chemistry (Figure 3). Concentrations of mobile trace elements in the vent fluids (e.g., B, K, Rb, Cs, Ba, Pb) increase from Kilo Moana southward to Tui Malila (and, for B, Ba, and Pb, southward to the Mariner vent field), consistent with a higher abundance of these elements in more slab-influenced felsic rocks. Differences observed for other elements (e.g., Fe, Mn, H₂S) are attributed to their being solubility-controlled species that are largely determined by temperature; concentrations of these species decrease from Kilo Moana to Tui Malila (as maximum temperatures of venting decrease from 333°C to 312°C), and then are significantly greater in Mariner vent fluids, which exhibit higher (up to 363°C) temperatures of venting (Mottl et al., 2011; Figure 4). Relative to all vent fluids from vent fields to the north, Mariner vent fluids sampled in 2005 (Mottl et al., 2011) and Vai Lili vent fluids sampled in 1989 (Fouquet et al., 1991) exhibit substantially higher

concentrations of CO₂, F (in excess of seawater), H₂S, and transition metals and are much more acidic (pH<2.8 at 25°C at Mariner in 2005; pH~2 at 25°C at Vai Lili in 1989; Figure 4). These more dramatic differences are consistent with magmatic volatile input and addition of acidity generated by disproportionation of magma-derived SO₂ (Mottl et al., 2011).

Vent deposit composition and morphology also differ from north to south, correlating with changes in rock and vent fluid chemistry. At the Kilo Moana and TowCam vent fields, high-temperature fluids exit from both open conduit “black smokers” and from “diffusers,” or “white smoker” spires that lack any large open conduits, and dominant minerals present (identified by X-ray diffraction and reflected and transmitted light petrography) include cubic cubanite (CuFe₂S₃; at Kilo Moana), chalcopyrite (CuFeS₂), and wurtzite ((Zn,Fe)S), with pyrite and marcasite (FeS₂) more prevalent in deposit exteriors, similar to chimneys found on MORs. At the Tahi Moana 1, ABE and Tui Malila vent fields, high temperature fluids exit both open conduit “black smokers” and “diffusers,” and slightly cooler fluids pool beneath flanges that protrude from either fault scarps or sulfide-rich edifices; dominant minerals include chalcopyrite and wurtzite, minor pyrite and barite (BaSO₄) and trace galena (PbS). The presence of barite and galena reflects enrichments of Ba and Pb in the vent fluids, from water-rock interaction with enriched igneous rocks. These minerals, and flanges, are also found in MOR deposits hosted in enriched MORBs (e.g., at Lucky Strike and Endeavour Segment vent fields; Tivey and Delaney, 1986; Langmuir et al., 1997; Tivey et al., 1999; Kristall et al., 2006). The presence of flanges at vent sites has been attributed to the presence of minerals that increase the structural integrity of deposits, such as barite, amorphous silica, and calcite, with the presence of amorphous silica attributed to high pH (relative to most MOR vent fluids)(Tivey et al., 1999). Abundant flanges were also observed at Kilo Moana vent field in 2009 (M.K. Tivey and A-L. Reysenbach, unpub.

data). At the Mariner vent field, high temperature fluids vent from the base and sides of tall (<10 to 27 m high), narrow (~3 to 4 m diameter) pinnacles, and lower temperature fluids emanate from tabular, squat edifices. High temperature Mariner chimneys are lined with chalcopyrite, and bornite and trace amounts of tennantite ($\text{Cu}_{12}\text{As}_4\text{S}_{13}$) are observed in mid- and exterior layers, with barite and minor sphalerite and pyrite, and trace galena, prevalent in the lower temperature squat edifices. The As-rich mineral tennantite has been observed in deposits from Vai Lili and other arc and back-arc vent fields, and reflects enrichments of As in vent fluid produced from interactions in a more felsic (relative to MOR) magmatic-hydrothermal system (Fouquet et al., 1991; Hannington et al., 2005). No high temperature venting (>121°C) was observed at the Vai Lili vent field in 2005, although thick layers (centimeters) of warm (~60°C) iron-manganese oxide mats reminiscent of those at Loihi Seamount (Glazer and Rouxel, 2009) were prevalent in the area. Trends observed in the bulk geochemical compositions of vent deposits from each vent field (M.K. Tivey, unpub. data) correlate with trends observed in vent fluid chemistry, with concentrations of Pb, Ba, As and Sb lowest in deposits from the Kilo Moana vent field and higher in deposits to the south, likely reflecting the influence of the host substrate on vent fluid compositions.

COMMUNITY ECOLOGY AT THE LAU ISS

Hydrothermal vents along the ELSC/VFR, like most hydrothermal systems, are populated by lush animal communities, a stark contrast to the otherwise barren surrounding seafloor (Fisher et al. 2007; Podowski et al. 2010). At depths well below the penetration of sunlight, reduced chemicals in vent fluids are the energy source that drives primary production through microbial chemosynthesis. As seen at other vents, the visually prominent individuals in animal communities at ELSC/VFR vents are typically dominated by animal-microbial symbioses,

namely invertebrates that form symbiotic associations with chemosynthetic bacteria (Cavanaugh et al., 2006; Dublier et al., 2008). At ELSC/VFR vents, the most abundant symbioses involve mollusks, mainly two genera of provannid snails and a bathymodiolid mussel (Desbruyeres et al. 1994; Podowski et al. 2010). The spreading centers are also home to numerous non-symbiotic invertebrates such as crabs, anemones, sea cucumbers, shrimp and barnacles (Desbruyeres et al. 1994; Podowski et al. 2010). The ELSC/VFR vent fauna are generally representative of the animal communities found at vent systems in its biogeographic province, such as the other western Pacific back-arc basins (e.g. Manus and North Fiji) and the Mariana trough (Ramirez-Llodra et al., 2007).

At vents, where microbial primary productivity is associated with vent fluid flow, organisms must often be exposed to diffuse vent fluids to support symbiont chemosynthesis or to access food such as free-living microbes. Thus, habitat preference is driven to varying degrees by a need for reduced chemicals or food, balanced by physiological or behavioral adaptations to the stress accompanying exposure to venting fluid. Biological interactions, such as competition for the limited space surrounding vent orifices, also plays a role in structuring vent communities.

Previous research in other vent systems has found that species are typically associated with particular physicochemical habitats, implicating both abiotic and biotic factors in affecting animal distribution (Fisher et al. 1988a; Fisher et al. 1988b; Le Bris et al. 2006; Luther et al. 2001; Moore et al. 2009; Shank et al. 1998). These studies have shed much light on those factors that govern the distribution of animals within a single site. As described above, the ELSC/VFR differs from other systems as it exhibits a diversity of chemical, thermal and geological attributes at both the local (vent field) and regional (along-axis) scale. Thus, the ELSC/VFR offers a

unique opportunity to examine how both local and regional gradients in the physical and chemical milieu affect faunal distribution.

How geological features influence megafaunal distributions in the Lau basin

Image-based analyses of diffuse flow megafauna communities have revealed regional-scale patterns of animal distribution along the spreading center that implicate geology as a primary factor influencing the presence of animals at each site (Podowski et al. 2009, 2010). The tendency for point source type emissions with limited horizontal dispersion from pillow basalts in the northern vent field diffuse flow communities contrasts with high spatial autocorrelation (inverse relationship between distance and similarity) of physicochemical parameters for more dispersed, horizontally extensive emissions from substrate (more crumbly andesites) in southern vent communities (Podowski et al. 2010). Podowski et al. (2010) hypothesized that these physical differences produce different small-scale flow regimes in the upper centimeters of the seafloor and strongly influence vent animal distributions among the four vent fields. For example, anemones can be quite dense on the northern basalts (Figure 5a), where the anemones may benefit from higher prey densities associated with enhanced chemosynthetic primary productivity in their immediate vicinity without exposure to toxic, high-temperature vent fluids.

The influence of vent fluid composition on the distribution of animal-microbial symbioses

Within the framework of a geographic information system, high-resolution photomosaics and discrete *in situ* electrochemical measurements of sulfide and oxygen concentrations were coupled with temperature measurements to examine animal distribution in relation to physicochemical data. The dominant symbioses in the ELSC/VFR, the white hairy snail *Alviniconcha* spp., the black snail *Ifremeria nautilei*, and the mussel *Bathymodiolus brevior*, are

mobile and can readily move as adults to seek out optimum local habitat. In both diffuse flow and chimneys across the region, these symbioses consistently distribute around vent orifices according to their differential tolerances to vent fluid exposure. Occasionally, this pattern qualitatively resembles a “bullseye”, in which *Alviniconcha* spp. occupy areas closest to the venting source (highest temperature and sulfide; lowest oxygen) and are, in turn, surrounded by *I. nautiliei* and mussels, corresponding to decreasing exposure to vent fluid (Figure 5b; Podowski et al. 2010; Podowski et al. 2009; Waite et al. 2008). This local pattern of distribution around venting fluid is consistent despite the decreasing amount of hydrogen sulfide in the endmember as well as diffuse vent fluids along the spreading axis from Kilo Moana to Tui Malila (see Figure 4; Mottl et al., 2011; Gartman et al., 2011; Luther et al., this issue). The mollusks occupy similar thermal regimes throughout the region, but are found in areas of decreasing hydrogen sulfide concentration from north to south. These data, along with shipboard experiments demonstrating tolerance to hydrogen sulfide concentrations well beyond those measured *in situ* (Henry et al. 2008), suggest that in the Lau basin the maximum exposure of the symbiont-containing mollusks to vent fluid is constrained by temperature tolerance, not sulfide toxicity. Biological interactions such as competition or facilitation are also implicated in determining the realized distribution of these animals where their physiological tolerances and requirements overlap (Podowski et al., 2010).

In the Lau basin, the differing chemical composition of vent fluid (end-member and diffuse) may drive the distribution of closely related vent symbioses along the spreading axis. Preliminary data from a study of *Alviniconcha* snail symbioses suggest that four different *Alviniconcha* spp. host types are found in the Lau basin, which form specific associations with three phylotypes of proteobacterial endosymbionts. These distinct holobionts (symbiont+host)

were found to differentially distribute along the spreading axis, varying in abundance from north to south (R. Beinart, unpub. data). Though these preliminary data suggest that north-south geochemical differences may influence the distribution and abundance of these symbioses, ongoing studies are aimed at better understanding precisely which factors govern the observed distributions.

Vent fluid geochemistry also likely plays a primary role in the distinctive composition of the animal community at the Mariner vent field. This site is populated by numerous reddish-brown black smoker chimneys, which lack the symbiotic mollusks that dominate the other sites (Figure 5c). Nevertheless, many of the non-symbiotic vent fauna (shrimp, crabs, polynoids, and limpets) occur here, indicating local microbial primary productivity. The absence of the symbioses may be attributable to higher concentrations of heavy metals such as manganese and iron in the vent fluids (Hsu-Kim et al. 2008; Mottl et al. 2011; Yücel et al., 2011) (see Figure 4), which bind to sulfide and might make it biologically inaccessible to the bacterial endosymbionts. To date, however, no studies have directly addressed why animal-microbial symbioses are absent from Mariner.

Characterizing microbial diversity along the Eastern Lau Spreading center

Understanding the nature and extent of microbial diversity at hydrothermal vents has been a long-standing objective of microbiologists. Oceanic ridge systems, which are discontinuous seafloor features residing in a more contiguous ocean, provide an opportunity to examine how microbial ecology is influenced by hydrological, geological, geochemical and biological factors across spatial and temporal scales. The aforementioned gradients in geology and vent fluid composition along the ELSC/VFR provide a natural setting for microbial diversity and ecology studies.

Using high throughput DNA sequencing approaches that provide both the depth and breadth needed to explore patterns of microbial diversity, some interesting insights are emerging concerning the microbial diversity of deposits along the ELSC/VFR. Most notably, the communities at Mariner are very different from others further north (Figure 6; A-L. Reysenbach, unpub. data). Additionally, from studies in 2009, communities from Kilo Moana deposits appear to be more different from those at TowCam, Tahi Moana, ABE and Tui Malila, while communities at ABE and Tahi Moana are most similar to each other (Figure 6; Flores et al., in review). These trends were apparent by taxa level associations (for example, among the Epsilonproteobacteria) and sequence level discrimination (operational taxonomic units) for both Archaea and Bacteria. Of interest is that these trends mirror the extent to which fluid compositions differ among the vent sites, with Mariner exhibiting the greatest differences in vent fluid pH, and Fe, CO₂ and H₂S concentrations, followed by Kilo Moana, with ABE and Tui Malila exhibiting greatest similarity (Figure 4; Mottl et al., 2011; Yücel et al., 2011). However, because of a relatively small set of vent deposits analyzed from Kilo Moana (four samples) and Tui Malila (three samples), these observations should be considered as preliminary, while those from Mariner, ABE and Tahi Moana are statistically robust.

Like at other vents sites worldwide, the Epsilonproteobacteria dominate the microbial communities associated with vents deposits along the ELSC/VFR. In sampled deposits, *Camnibacter* spp. were more prevalent at Mid-Atlantic Ridge vents (Flores et al., 2011), with the diversity of Epsilonproteobacteria very different along the ELSC/VFR. Members of the *Lebidomonas* (moderate acidophiles) were more prevalent at all ELSC/VFR vent fields with a shift to the anaerobic Nautiliales (represented by *Nautilia*) at Mariner (Flores et al., in review),

which also drive the notable differences between Mariner and the other vent sites along the ELSC/VFR (Figure 6).

In addition to composition of the Epsilonproteobacteria, the archaeal composition differed between deposits from Mariner and the other ELSC/VFR sites (this study). All sites, except Mariner, exhibit a rich diversity of Crenarchaeota, with the prevalence of members of the hyperthermophilic Desulfurococcaceae (*Aeropyrum*-related) and Thermofilaceae. It is notable that *Thermofilum*-type isolates have rarely been isolated and only sometimes viewed in enrichments (Reysenbach, personal observation). In contrast, Thermococcales dominate the archaeal communities of many of the deposits at Mariner (Takai et al 2008; Flores et al., in review). This is interesting as cultivated Thermococcales are generally hyperthermophilic heterotrophs utilizing a wide range of complex organic compounds. The Mariner Thermococcales may be carboxydolithotrophs by capitalizing on the high CO₂ (and CO) by CO-oxidation (see Figure 4), as has been reported for a close relative isolated from the PACMANUS vent field in the Western Pacific (Lee et al., 2008). Furthermore, numerous sequences never previously obtained from deep-sea vents have been obtained from vent deposit samples from Mariner. These sequences are all affiliated with extremely acidophilic microbes associated with terrestrial solfataras (Reysenbach et al. 2006).

The ELSC/VFR vent fields have also been a hotbed for novel cultivated thermophiles. Isolates from Mariner provided the first glimpse of the physiology of the deep-sea vent endemic taxonomic clade, “DHVE2” (Reysenbach et al., 2006), now named *Aciduliprofundum boonei*. This organism was the first thermoacidophile detected from deep-sea vents and its genome has been sequenced (Reysenbach and Flores, 2008) and completed (NCBI # [NC_013926](#)). Additional members of the “Aciduliprofundales” have been isolated from vents along the East

Pacific Rise and Mid-Atlantic Ridge (Flores et al., in revision). Furthermore, other new thermoacidophiles isolated from the ELSC/VFR vents are members of the Deltaproteobacteria, the first members of *Hipaea* from deep-sea vents (Flores et al., 2011) and first thermoacidophilic *Hipaea* species. Among the other novel genera isolated from ELSC/VFR vent deposits are *Thermosulfurimonas dismutans*, a thermophilic sulfur-disproportionating bacterium from Mariner, and *Deferrisoma camini*, a moderately thermophilic dissimilatory Fe(III)-reducer from ABE (Slobodkin et al., 2011; Slobodkina et al., 2011).

SUMMARY AND CONCLUDING REMARKS

Water enables Earth's surface to support life, and enhances the convective vigor of Earth's interior, supporting and perhaps enabling plate tectonics. The study of the ELSC/VFR also shows the importance of water to the operation of the ridge system, from mantle to microbe to megafauna. Because of the location of the spreading center above a subduction zone, the underlying mantle receives an increased flux of water and other elements transported from the subducting slab (Figure 0). In turn, water lowers the mantle melting temperature and leads to greater melt production where the water flux is greater. Higher water content in the mantle source region is coupled with increased concentrations of other elements such as K, Ba, and Pb, influencing the chemical composition of hydrothermal fluids and the mineralogy of hydrothermal deposits.

Because the influence of the subducting slab increases north to south, there are corresponding increases in water and other slab-derived elements in the mantle source region that are reflected by physical changes in the crustal properties along the spreading axis. Additionally, the dynamic effect of the slab in the mantle may also be important in enhancing magma production, as numerical geodynamic models suggest that there may be greater

upwelling leading to decompression melting with faster subduction (Harmon and Blackman, 2010). The enhanced magmatism at the southern end of the ELSC/VFR leads to thicker crust and a domed ridge axis, in contrast with the rifted ridge of the northern ELSC. Higher water in the magma leads to crystallization trends that make the crust richer in silica. The water also exsolves and creates bubbles in the magma as it ascends through the crust. Vapor bubbles may promote greater porosity and influence fluid flow in the crust, and also influence the crustal density and physical properties. It has been hypothesized that these physical changes may influence the extent of very shallow dispersed versus focused fluid flow, creating different habitats for biological communities.

The north-south differences in mantle-source water and elemental content also manifest in a regional-scale gradient in vent fluid geochemistry, which is relevant to the biological communities found along the spreading axis. Concentrations of mobile trace elements in the vent fluids (e.g., Ba, Pb) increase from Kilo Moana southward to the Mariner vent field, consistent with a higher abundance of these elements in more slab-influenced felsic rocks. Where water is highest and the effects on differentiation most extreme, the exsolved magmatic H₂O, CO₂, and SO₂ may, as in the Mariner vent field, rise and join with circulating hydrothermal fluids and profoundly change the chemistry of vent fluids in ways that never happen on mid-ocean ridges. The resulting more acid fluids can react with the underlying rocks and dissolve more transition metals. These chemical differences can result in striking geochemical differences for fauna, as observed at the Mariner vent field (Takai et al., 2008).

In total, the Lau ISS' distinctive regional-scale gradients in physical and chemical properties have revealed exciting linkages between subsurface processes and deep-sea biological processes, and underscore the degree to which subsurface physical and chemical phenomena can

drive biological processes. Indeed, the influence of the subducting slab is transmitted from the mantle to the seafloor, profoundly affecting the hydrothermal vent ecosystems in this region. Gradients in the composition of the hydrothermal fluids, mineral components, and structure of vent deposits result in different habitats for biological organisms at a regional scale. At the Lau ISS, R2K studies have documented that biological communities, both microbial and animal, clearly are shaped by mantle-derived processes. The totality of studies carried out at the Lau ISS, that traverse the disciplines of the ocean sciences, further demonstrates the causal linkages that operate at spreading ridges, and that extend from the mantle to microbes at the seafloor.

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Add Fornari et al., 2012; Kelley et al., 2012; Speer and Thurnherr 2012, Lau Workshop Report, 2006; Tivey et al., 2005;

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FIGURE CAPTIONS

Figure 1. (a) Vent field locations (red dots) along the ELSC/VFR in the Lau Basin. Map created using GeoMapApp (Ryan et al., 2009). KM is Kilo Moana, TC is TowCam, TaM is Tahi Moana, TM is Tui Malila, Ma is Mariner, VL is Vai Lili. (b) Multibeam bathymetry of the ELSC/VFR (first panel) showing the locations of vent fields (diamonds), and selected across-axis topographic profiles. Second panel shows the axial depth profile along the ELSC/VFR and optical backscatter values relative to background measured with up to 8 MAPR instruments during deep-towed sonar surveys. NTU values are compiled from multiple tows generally offset about 300 m to each side of the axis (colors are gradational from Δ NTU 0.010 to 0.015 (blue) to 0.070 to 0.080 (red)). Black vertical bars delimit extents of the VFR, C-ELSC, and N-ELSC and are annotated at ends with the spreading rate and distance to the arc volcanic front. Bars along the right edge indicate where magma lens reflectors are (green bar) and are not (open bar) identified from [Harding et al., 2000](#). The third panel shows sonar imagery from ship EM120 multibeam system, with dark shades indicating high backscatter. The fourth panel shows the distribution of near-axis large faults identified both in sides-scan imagery and bathymetry. White area shows approximate limits of coverage considered in the fault identification. Red line is the ELSC axis location. After Martinez et al. (2006).

Figure 2. Changes in compositions of erupted lavas with location along axis. Color changes with each segment. (a) MgO (wt.%), which corresponds closely with magma temperature; (b) Ba/Th; (c) Th/La. Ba, Th, and La are trace elements that are associated with fluxes from the down-going slab. Note from the different characteristics of the Ba/Th and Th/La profiles that there is not a simple two component behavior. Multiple slab components that vary along the arc are

necessary. Data from Bezos et al. (in prep.), Bezos et al. (2009), and Escrig et al., (2009).

Figure 3. Correlations between igneous rock composition and vent fluid chemistry. Note that ratios with Li are far better correlations than elements alone, which would be expected since ratios are independent of fluid mass and water/rock ratio. Rock data are from Bezos et al. (in prep.), Bezos et al. (2009) and Escrig et al. (2009). Fluid data are end member compositions from Mottl et al. (2011), averaged for each vent area. mm is millimoles/kg, ppm is parts per million.

Figure 4. Ranges of temperature, pH measured at 25°C, and zero-Mg end-member Fe, H₂S, and CO₂ for low Mg (<10 mmol/kg) vent fluid samples collected in 2005 for Kilo Moana (KM), TowCam (TC), ABE, Tui Malila (TM) and Mariner (MA) vent fields, and in 1989 for Vai Lili (VL). After Mottl et al., 2011. Vai Lili data from Fouquet et al., 1993.

Figure 5. (a) Anemones are common and often quite dense on the pillow basalts of northernmost vent fields along the Eastern Lau Spreading Center. The anemones reside in close proximity to vent flows where they can access higher prey densities supported by enhanced local primary production..(b) A canonical “bullseye” assemblage of *Alviniconcha* spp. snails shown in the middle, surrounded by *Ifremeria nautilei* snails and *Bathymodiolus brevior* mussels. *Alviniconcha* spp. occupy the region of greatest exposure to vent fluid. (c) Mariner field vents exhibit ample fluid flow but do not host any of the chemoautotrophic symbioses commonly found within the Eastern Lau Spreading Center, likely due to substantial differences in vent fluid geochemistry.

Figure 6. Relationships of the bacterial communities associated with vent deposits sampled in 2009 from the different vent sites along the ELSC/VFR, and Mid-Atlantic Ridge (branches nearer to each other are more closely related). Note that Mariner bacterial communities are more different in composition from all other sites, while communities from ABE and Tahiti Moana cluster together. Furthermore, ELSC/VFR sites are more similar to each other than to Mid-Atlantic Ridge sites, Lucky Strike and Rainbow, providing evidence for an emerging biogeography of bacterial communities associated with hydrothermal deposits. These similarities among ELSC/VFR communities mirror relative similarities in pH, Fe, H₂S, and CO₂ for fluids sampled in 2005 (Figure 4; Mottl et al., 2011). Compositions of vent fluids sampled in 2009 are similar to those sampled in 2005 with some exceptions at the Kilo Moana and Mariner vent fields. In 2009, H₂S concentrations at some vents at Mariner exceeded measured values in 2005 samples, and Fe and H₂S concentrations at Kilo Moana were significantly lower than measured values in 2005, with H₂S concentrations similar to those at TowCam vent field (in both 2005 and 2009), but with Fe concentrations still slightly higher at Kilo Moana than at TowCam vent field (J. Seewald, C.G. Wheat, pers. comm.). The 16S rRNA gene pyrotagged sequence diversity of multiple samples collected from each vent field was combined to reflect the overall diversity of each vent field. Cluster analysis was done using the Bray Curtis similarity index using Primer-6 software package.